Seasonal Changes in Respiratory Rate of Stems and Their Growth*

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幹の呼吸速度と幹の生長の季節変動

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CONTENTS

RÉSUMÉ

The relation between respiratory rate per month in stem samples and their growth rate were investigated relating to the seasonal change. The following results were deduced.

1) Respiratory rate per month in the stem samples had a close relation with the growth of the stems during a growing season.

2) During a dormant season, the rate of respiration is proportional to the surface area of the stem samples.

3) In the relation between respiratory consumption per year in the stem samples (R) and growth of the volume ($\varDelta V$) or growth weight ($\varDelta W$) in a current year, following relations were found, i. e.,

$$\log R = 0.681 \log \varDelta V + 0.302$$
$$\log R = 0.682 \log \varDelta W + 0.326$$

要　　旨

幹の呼吸速度と幹の生長速度との関係が，呼吸速度の季節変化に関連して調べられた。その結果は次のようにまとめられた。

1) 生育期における一カ月当りの呼吸量は一カ月当りの幹の生長量と密接な関係を持つ。

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2) 休眠期における呼吸速度は，幹の表面積に比例する関係にあった。

3) 一年間の幹の呼吸量と幹の生長量との関係は，比例関係ではなく，次の式が近似された。

$$\log R = 0.681 \log \Delta V + 0.302$$

$$\log R = 0.682 \log \Delta W + 0.326$$

INTRODUCTION

In lower living things, the physiological mechanism of the control of the environments seems to be comparatively simple in comparison with that of higher plants, therefore the soil respiration of each month may be estimated only from the relation with the mean temperature of the month[1),2)]. On the other hand, the respiratory consumption of trees seems to have some patterns of seasonal change, pattern which is a little different from that of rhythm of the mean temperature of the month. The difference of the patterns must be treated carefully when the respriatory consumption of trees is estimated reasonably.

Although the relation between the growth of stems and the respiratory consumption was often pointed out in the past, in most cases, it was not investigated in connection with the estimation of the respiratory consumption. Seasonal change of the respiratory rate of stems may be taken into account for the estimation of the consumption, because of the reason mentioned above.

In this report, the relation between the seasonal change of growth of a part of a stem and that of respiration was treated in connection with the estimation of respiration of one year.

MATERIALS AND METHODS

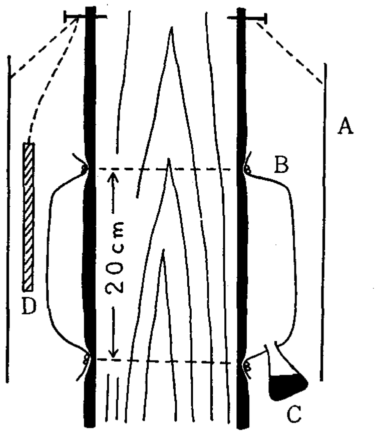

Fig. 1. Apparatus of measurement of respiration. A: cover for shading, B: polyvinylchloride film for respiration chamber, C: KOH solution for absorption of CO_2, D: maximum-minimum thermometer.

Experiment 1

The trees investigated were selected from two parts of the botanical garden on the campus of Kyoto University and from the natural stand of *Pinus densiflora* at Kamigamo Experimental Forest Station of Kyoto University. The species of trees examined at the botanical garden were 5 broad-leaved trees and 1 deciduous coniferous tree. At Kamigamo Experimental Forest, the species of tree selected were mainly *Pinus densiflora* (10 samples).

Measurement of respiration was taken from April 1968 until January 1969. At Kamigamo Exp. Forest, two measurements were made, the one was the measurement of respiration, and the other was the measurement of the growth of the diameter of the stems.

Stem samples to measure respiration were wrapped with polyvinylchloride film 20 cm long at 1 m above the ground. A 0.5 N KOH bottled solution was used for absorption of carbon dioxide (Fig. 1). The amount of KOH solution was changed by the different amount of carbon dioxide evolved during the season.

Measurement of respiration was practiced under natural conditions for 24 hours, once a month throughout the season. Maximum-minimum thermometers were placed to estimate the mean temperature during the period of measurement.

To estimate the growth of diameter of stems, simple apparatus were set up near apart of the stems to measure the respiration, and the measurement was taken from April to January. At the end of the measurement period the growth of the diameter was again measured by an increment borer.

Experiment 2

The trees investigated were selected from artificial plantation forests of *Cryptomeria japonica* (13 sample trees) and *Tsuga Sieboldii* (11 sample trees) at Kamigamo Exp. Forest Station.

The respiratory rates were measured by the same method of Exp. 1. The experiment was practiced from April 1969 to January 1970. The growth of the diameter was measured in February 1970, when the respiratory measurement ceased to change.

RESULTS AND DISCUSSION

1) Seasonal change of the growth of the diameter and volume of the stems.

The growth of the stems in diameter investigated begins in April before the trees sprout, and reaches maximum in early summer, and ceases in September or October. These patterns of the growth of diameter were the same for all three species, in spite of the differences of the life patterns of the trees.

K. Kuroiwa[8] and others pointed out that the daily rate of the growth of stem diameter of *Pawlownia tomentosa,* a deciduous broad-leaved tree, was in close relation with the values of change of air temperature at respective days, and reported that the growth of the diameter was affected not only by the season but also by every day wheather.

N. Tsuda and K. Shimaji[9] examined the seasonal change of the number of immature tracheid layer of stems of *Pinus densiflora,* and reported that the number of immature tracheid layer of mature trees attained to a maximum in April or May and declined gradually till early winter.

The rough patterns of the growth of the diameter of stems in this present experiment had the same results as in the experiments mentioned above. The patterns of the seasonal change of the volume growth of stems may be likely to that of the diameter because the growth of diameter was small in comparison with the diamter of the stem sampled. The volume growth of the stem begins in mid April, reaches maximum in early summer, and declines gradually until autumn (Fig. 2).

2) Seasonal change of the respiratory rate of stems.

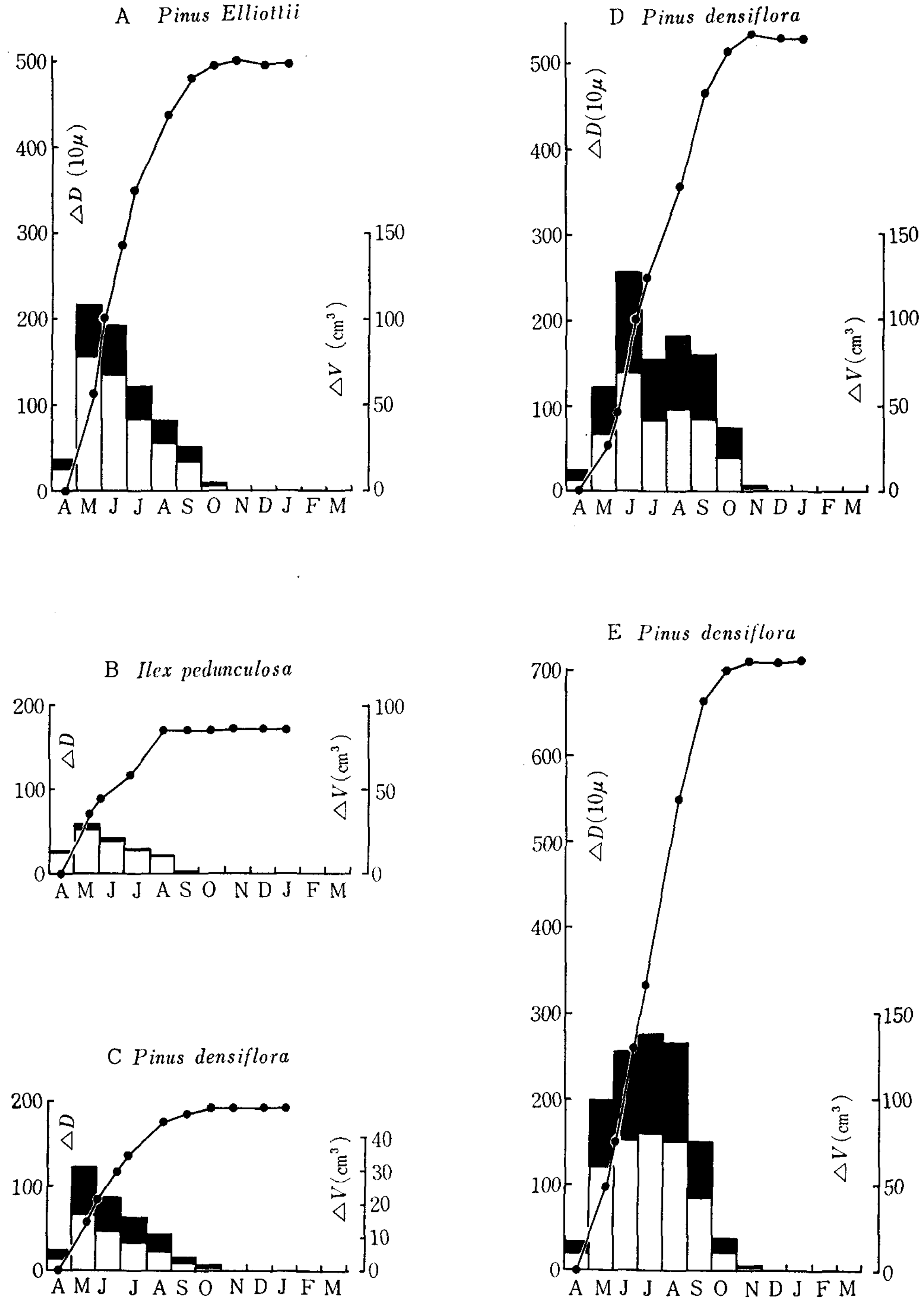

Fig. 2. Seasonal changes in growth of diameter; growth rate per month (ΔD) and growth rate of stem volume (ΔV) in some species examined.

The seasonal change in respiratory rate of stems was shown by the curves in Fig. 3, in which the rate had maximum in early summer. For convenience, the amount of respiration was expressed in grams of CO_2 taken monthly from samples in Fig. 3. The patterns

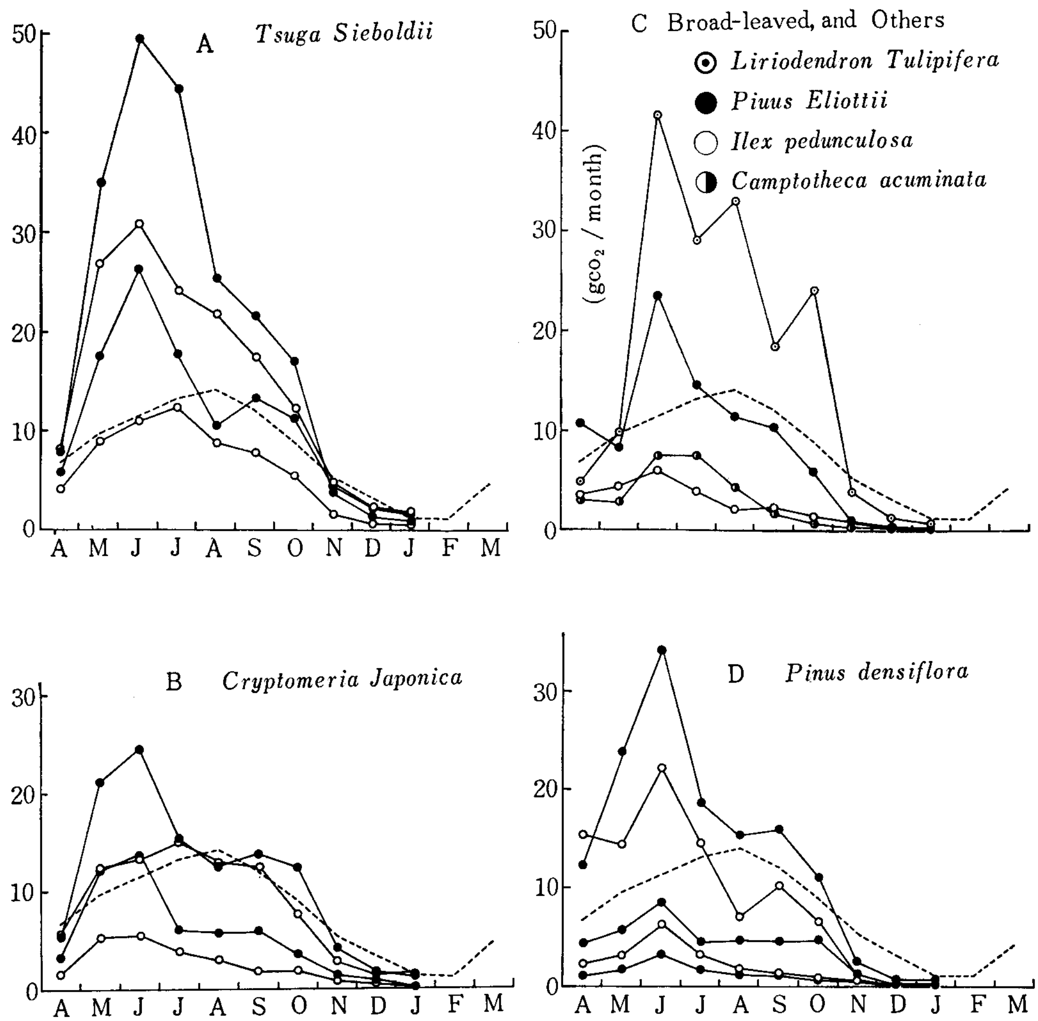

Fig. 3. Seasonal changes of respiratory rate of stems of some species.

of the curves of the changes were similar to those of the previous works reported for several tree species by N. Johansson[4] and for scarlet oak by B. M. Woodwell and D. B. Botkin[3], in which the respirations were measured by a similar apparatus set up on the stems of forest trees.

The patterns of the rate of respiration were different from the curves of the mean temperature of the month. The rough patterns of the seasonal change of the rate of respiration were more or less the same as the patterns of the volume growth of the stems.

From the data of Exp. 1, simple correlation coefficients were calculated from the relation between respiratory rate (gr CO_2/month/sample) and volume growths (cm^3/month/sample)

Table 1. Simple correlations between rate of respiration per month (r) and volume increment per month (Δv) during growing season.

Month	Simple correlation(r)	r^2
4	0.5261*	0.2768
5	0.6257*	0.3915
6	0.9058**	0.8205
7	0.7984**	0.6374
8	0.7583**	0.5750
9	0.8628**	0.7444
10	0.6913**	0.4779
11	0.3695*	0.1365

* significant at $P<0.05$.
** significant at $P<0.01$.

among 5 species, 14 sample trunks in certain growing season. The result was tabulated in Table 1, and 2, in which the relation seemed to be intimate between them during the growing season from June to October. This relation may correspond to the productive respiration named by N. Johansson.

Although the simple correlation analysis cleared the realtion between them by a significant 99% level, the result may be effected by the factor of temperature. One statistical analysis was used for the examination of the effects of the temperature, the values of partial correlation coefficient were calculated among the values of logarithm of respiration per month, values of logarithm of growth of the stems and mean temperatures of the month in the growing season of trees (Table 3). As the respiratory rate seems to rise exponentially with the temperature, the value of the respiration was converted into the value of the logarithm and the value of the growth was equally converted from the relation to the respiration in the analysis. The analysis of the partial correlation coefficient seem to mean that the relation between the respitation and the growth of stems, between the temperature and the growth, and between the temperature and the respiration during the growing season were the highest, although the variances among the values were large.

Table 2. Simple correlations between rate of respiration per month (r) and volume increment per month (Δv) in respective samples during growing season.

Species	Diameter (cm)	Correlation coefficient (r)	r^2
Pinus densiflora	5.35	0.7310**	0.5344
Pinus densiflora	5.85	0.7859**	0.6176
Pinus densiflora	6.25	0.8816**	0.7772
Pinus densiflora	7.65	0.6122**	0.3748
Pinus densiflora	11.45	0.7742**	0.5994
Pinus densiflora	14.50	0.6983**	0.4876
Pinus densiflora	15.35	0.7404**	0.5482
Pinus densiflora	20.00	0.7118**	0.5067
Paulownia tomentosa	16.15	0.8217**	0.6752
Ilex pedunculosa	8.30	0.6876**	0.4728
Quercus serrata	9.40	0.7449**	0.5549
Quercus serrata	10.80	0.7405**	0.5483
Pinus Elliottii	11.90	0.6863**	0.4710
Pinus Elliottii	13.55	0.7648**	0.5849
mean		$\bar{r}=0.7415$	$\bar{r}^2=0.5537$

** significant at $P<0.01$.

Although it was calculated that the respiratory rate of the stems has an intimate correlation with the growth rate in the growing season of trees, there was no enucleation for

Table 3. Correlations between logarithm of rate of respiration per month(r), logarithm of volume increment per month (g) and mean temperature of month. r_{rg} etc. mean partial correlation coefficient between log r and log g, etc.

Species	r_{rg}	r_{rt}	r_{gt}
Pinus densiflora	0.8572*	−0.4981	0.7517
Pinus densiflora	0.9346**	−0.1138	0.3185
Pinus densiflora	0.1248	−0.0042	0.3143
Pinus densiflora	0.7370	−1.1925	0.6691
Pinus densiflora	0.6830	0.1359	0.3888
Pinus densiflora	0.1981	0.1521	0.7806*
Pinus densiflora	0.8419	0.1807	−0.4143
Pinus densiflora	0.7066	−0.2091	0.7447
Paulownia tomentosa	0.8967**	−0.7336	0.9279**
Ilex pedunculosa	0.5242	0.2559	0.4005
Quercus serrata	0.7132	−0.4270	0.3643
Quercus serrata	0.1679	−0.5551	0.6177
Pinus Elliottii	0.4990	−0.0410	0.5395
Pinus Elliottii	0.6937	−0.4453	0.5755
mean value	0.6127	−0.1782	0.4984

* significant at $P<0.05$.
** significant at $P<0.01$.

the other season in the analysis mentioned above. The relation between the respiratory rate and size of the sample of individual trunks in a forest may be effective to answer the purpose, which was already discussed in the past.

Between the respiratory rate (r) and diameter of the trunk (D) in a forest trees, the following equation was found, i.e.,

$$\log r = a \log D + b,$$

where (a) and (b) are constants. The constants (a) and (b) change seasonally. If the gradient value of (a) be equal to 2.0, 1.0, and 0.0, then the respiratory rate in the stems may be expected to be proportional to the volume, to the surface area or have no relation with the diameter respectively. The values of the (a) were calculated by the method of least square and were shown in Fig. 4. The change of the gradient value of the equation

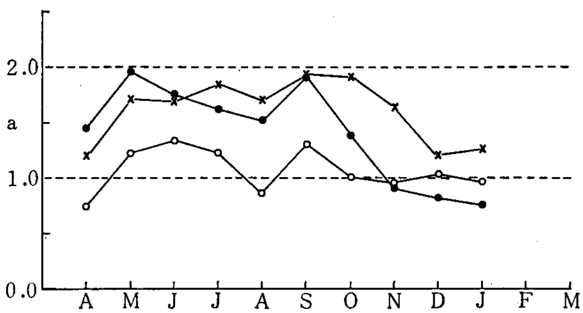

Fig. 4. Seasonal changes in gradient value of equation (1). Dots: *Pinus densiflora*, saltirecross: *Cryptomeria japonica*, circles: *Tsuga Sieboldii.*

seemed to show the characteristics of seasonal changes of respiratory rate of stems. The gradient values were approximated to 2.0 during growing season in the stems of *Pinus* *densiflora* and *Cryptomeria japonica,* and to 1.0 during dormant season in three species examined. From this result, the respiratory rate of stems may be proportional to the surface area of the stems during the dormant season, and the phenomenon may be shown in directly the activity of cambium of the stems in the season.

3) Relation between the amount of respiration per month and the growth of the stems

Estimation of the amount of respiration in the non-photosynthetic organ of trees is a difficult problem because the respiratory rate changes not only daily but also seasonally. Thickness of stems or stem weight has been used for the estimation of the amount of respiratory consumption of a tree relating to the respiratory rate of one growing season. Despite its usefulness, some serious difficulties may be involved in the method of estimation. If the respiratory consumption be treated for a whole year, the problem of the effect of seasonal change may disappear. For this reason, the amount of respiration per year (R) of respective sample stems was treated relating to the volume of the stem samples (V).

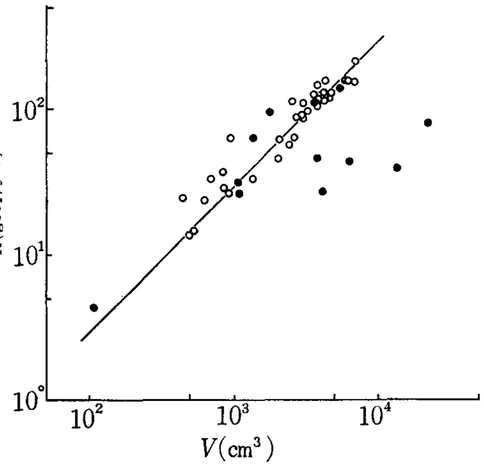

Fig. 5. Amount of respiration in stems and volume of stems. Dots: broad-leaved species, circles: coniferous species.

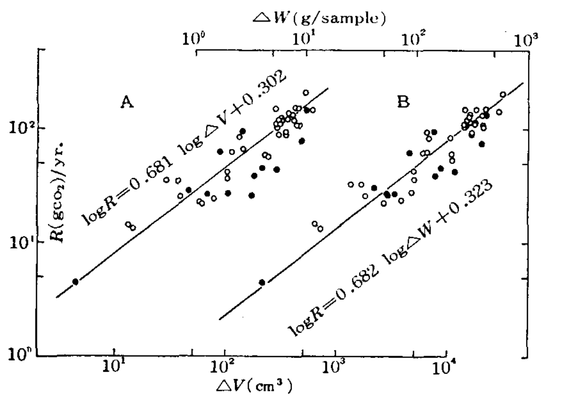

Fig. 6. Amount of respiration and growth of volume in a current year (A), and Amount of respiration and growth of weight in a current year (B). Dots: broad-leaved species, circles: coniferous species.

According to the study made above, the following may be expected, the respiratory consumption of each sample was not proportional to the volume of the stems (V) as they were. The log V—log R relation was shown in Fig. 5, in which the observed values were scattered in a wide zone. As the respiration of stems is mostly concentrated in the thin cambial zone, the large volume of the wood does not always mean an evolvement of large amount of carbon dioxide.

A close correlation between log $\varDelta V$ and log $\varDelta R$ was recognized among respective stems regardless of their species or tree age, but the deviation of the points from the regression line was relatively large (Fig. 6A). The deviation of the regression line can be measured a little by converting the growth of the volume during a current year ($\varDelta V$) into growth of weight ($\varDelta W$) from the conversion factors of specific gravity of trees (Fig. 6B).

The constants of the regression line were tentatively calculated by the method of least square, and they were estimated as follows:

$$\log R=0.681 \log \Delta V+0.302 \quad (1)$$

$$\log R=0.682 \log \Delta W+0.323 \quad (2)$$

The gradients of Eq. (1) and Eq. (2) is very near to 2/3, which may indicate that the respiratory consumption is proportional to the surface area of the growth volume of the stems during a current year. If the respiratory consumption be proportional to the amount of the growth in a current year as expected during a growing season, the gradients must have the near value of 1.0. Though the respiratory rate of the month during a growing season was related to the growth rate of the stems, the amount of respiration of one year is effected by the other factors. The effect of temperature may be large.

The respiratory consumption of the respective stems may be divided into two amounts of respiration calculating the amount of respiration depending only upon the temperature under the assumption that Q_{10} is equal to 2.0. At the base of the estimation, respiratory rate during a dormant season was used in this calculation, which was suggested by N. Johansson. In here, the amount of respiration for one year (R) partitioned into two was defined for convenience. That is to say, the dormant respiration (R_d) is the amount of respiration for one year calculated by the relation between temperature and respiratory rate during a dormant season, and in productive respiration (R_p) there is a difference between R and R_d. When the log R_p—log ΔV or log R_p—log ΔW relations were compared, their gradients neared to 1.0.

The results discussed above seem to indicate that the mechanism of phenomenon of respiratory consumption in the stems are related to their growth. The respiratory reaction is a chemical one, so the amount of reaction may be reflected by the amount of chemical reaction in the stems.

Though the estimation of respiratory consumption of non-photosynthetic organs is a troublesome, the present relation of Eq. (1) and Eq (2) may be useful for this purpose, although the relation was still an empirical one.

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